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Vitamin A, Carotenoids and Total Lipids in the Livers of some Elasmobranchs

By L. R. FISHER, B.Sc., Ph.D.,
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May, 1964

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Vitamin A, Carotenoids and Total Lipids in the Livers of some Elasmobranchs

INTRODUCTION

In a recent account of vitamins in fish Higashi (1961) stated that "vitamin A is remarkably concentrated in the liver of fish". Liver oils from certain species of fish, both bony and cartilaginous, are still commercial sources of vitamin A in some parts of the world, despite the modern production of synthetic vitamin A. Schmidt-Nielsen *et al.* (1934 *a*, *b*) showed that the livers of elasmobranchs were larger than those of teleosts in relation to body size and were also richer in oil so that elasmobranchs with livers rich in vitamin A would be a more valuable source of the vitamin than teleosts and might prove worthy of commercial development.

Some years ago the possible commercial exploitation in the Scottish fisheries of the porbeagle shark, *Lamna cornubica*, was under consideration, and information about the potentiality of the liver oil as a source of vitamin A was required. This investigation was subsequently extended to a study of the vitamin A, carotenoid and lipid in the livers of various species of elasmobranch caught by Scottish research ships. The collection of livers continued from March 1954 until February 1962, some 429 livers from 31 species being analysed.

The author is grateful to Dr. B. B. Rae and other members of the staff of the Marine Laboratory of the Department of Agriculture and Fisheries for Scotland, not only for organising the collection of the material but also for their helpful criticism and advice during the preparation of this paper. The analyses were done in the Unit for Biochemical Research bearing on Fisheries' Problems (grant-aided by the Development Fund) at the National Institute for Research in Dairying, Shinfield.

There is no record that the liver oils of eight of the species have previously been analysed for vitamin A and relatively little recent work has been reported on the remaining species from seas around and north of the British Isles. The vitamin A activity of the liver oils in a number of elasmobranchs taken in the Norwegian fisheries was measured by Schmidt-Nielsen and his colleagues, first by biological assay with rats (Schmidt-Nielsen & Schmidt-Nielsen, 1927, 1929, 1930*a*, 1930*b*) and later by the Carr-Price colorimetric reaction (Schmidt-Nielsen & Schmidt-Nielsen, 1931; Schmidt-Nielsen *et al.*, 1934*a*). Some species from British fisheries were analysed by Lovern and his co-workers, who made spectrophotometric determinations of vitamin A on extracts of whole oils and on unsaponifiable fractions (Lovern *et al.*, 1933, 1939; Edisbury *et al.*, 1938). No attempt was made in any of these early investigations to separate vitamin A by chromatographic means from carotenoids or substances interfering with the physical or chemical measurements.

Since 1945 the liver oils of only a few species taken in seas fished by British vessels have been analysed; they include the basking shark *Cetorhinus maximus* (Davies & Worden, 1953-4), the long-nosed skate *Raia oxyrhynchus*, the spur dog *Squalus acanthias* (Lambertsen & Braekkan, 1956), and the Greenland shark *Somniosus microcephalus* (Aure & Kløkstad, 1951; Carlson, 1958; Lambertsen & Braekkan, 1956). Earlier analyses of liver oils of some of the species mentioned in this paper from other sea areas are referred to throughout the text.

MATERIAL

The livers were taken from fish caught mainly in Scottish waters by Scottish fishery research vessels and occasionally by Aberdeen trawlers and great-liners. The fish were identified and their maturities assessed by Dr. B. B. Rae of the Marine Laboratory or by members of the Laboratory staff working under his supervision. The nomenclature follows that of the "List of British Vertebrates" published by the British Museum (Natural History) in 1935.

TABLE I

LIPID, VITAMIN A AND CAROTENOIDS IN THE LIVERS OF SHARKS AND DOGFISHES (SELACHII)

Species	Sex	No. of livers analysed	Liver lipid (%)	Vitamin A		Carotenoids	
				μg/g liver	μg/g lipid	μg/g liver	μg/g lipid
Hexanchus griseus	♂	2	52 (50-55)	147 (95-227)	280 (173-454)	0·7 (0-1·8)	1·1 (0-3·5)
	♀	9	56 (31-82)	48 (20-137)	85 (31-219)	2·1 (1·0-3·4)	3·7 (1·9-6·4)
Carcharinus glaucus	♂	1	41	515	1286	1·2	3·0
	♀	2	41 (40-42)	189 (175-205)	463 (417-515)	1·7 (1·2-2·3)	4·1 (3·0-5·6)
Cetorhinus maximus	♂	2	66 (61-71)	31 (29-32)	46 (45-48)	3·1 (1·5-6·3)	4·6 (2·1-10)
Eugaleus galeus	♂	9	48 (31-88)	696 (91-5060)	1864 (189-13350)	4·9 (0·7-8·2)	10 (1·3-24)
	♀	3	38 (23-52)	213 (46-547)	552 (97-1665)	2·0 (1·0-6·2)	5·4 (2·2-12)
Lamna cornubica	♂	17	39 (3·6-82)	66 (17-568)	167 (20-3380)	5·1 (1·3-19)	13 (2·3-161)
	♀	11	42 (10-91)	35 (6·5-449)	85 (7·3-4444)	5·5*(1·6-22)	13* (1·8-113)
	not known	1	89	201	213	4·5	4·8
Mustelus mustelus	♀	3	45 (32-80)	34 (1·6-293)	163 (45-916)	3·3 (1·6-4·8)	7·5 (2·0-15)
Pristiurus melanostomus	♂	8	45 (12-78)	15 (0·3-92)	33 (2·5-304)	3·0 (2·1-5·0)	6·7 (2·8-29)
	♀	6	43 (25-78)	13 (3·3-32)	31 (6·9-96)	3·8 (2·2-7·3)	8·8 (4·2-29)
Scyliorhinus caniculus	♂	12	41 (15-71)	20 (3·5-121)	59 (8·8-234)	12 (5·0-95)	30 (7·1-182)
	♀	22	32 (3·2-71)	20 (2·9-226)	64 (5·8-538)	7·9 (3·2-26)	25 (5·2-232)
Centrophorus squamosus	♀	1	17	6·4	36	2·4	14
Centroscyllium fabricii	♀	1	32	100	304	2·7	8·5
Centroscymnus coelolepis	♂	2	63 (63-63)	28 (8·2-99)	45 (13-156)	0·6 (0·25-1·6)	1·0 (0·4-2·5)
	♀	1	29	11	39	2·9	9·9
Etmopterus spinax	♂	4	87 (80-95)	86 (16-376)	98 (20-397)	2·7 (1·0-6·7)	3·2 (1·1-8·0)
	♀	8	59 (30-91)	23 (5·2-158)	39 (8·4-172)	1·7 (0-5·3)	2·7 (0-14)
Scymnodon jonsonii	♀	1	38	14	35	4·0	10
Scymnorhinus licha	♀	1	67	43	64	0·7	1·0
Somniosus microcephalus	♀	1	47	279	600	1·6	3·4
	not known	2	53 (42-67)	277 (217-353)	522 (325-837)	2·8 (1·3-5·9)	5·1 (3·0-8·8)
Squalus acanthias	♂	44	37 (0·5-91)	28 (1·3-430)	70 (4·7-7460)	2·2 (0-8·0)	5·1 (0-1150)
	♀	45	47 (7·2-89)	43 (2·1-1347)	94 (9·0-5100)	2·2 (0-35)	4·2 (0-102)
Squatina squatina	♂	1	25	59	234	7·7	31
	♀	8	34 (19-58)	27 (7·2-87)	85 (28-244)	13 (3·6-42)	42 (12-106)
	not known	1	92	173	187	23	25

*Value for 10 livers only

Livers collected on the research vessels were preserved by immersion in pure ethanol within an hour of the fish being brought on board. Samples were then stored in a refrigerator until packed for transit by rail from Aberdeen to Shinfield, where they were kept in a deep-freeze at −20°C before analysis. Livers taken from fish caught by commercial fishing vessels remained unpreserved, except for the usual icing precautions, for periods varying from a few hours to two weeks or more; at Aberdeen they were subsequently preserved in ethanol. When possible whole livers were analysed, but if these were too large representative portions were taken. In some instances, two or more portions of a single liver were preserved and analysed separately.

ANALYTICAL METHODS

The ethanol was drained from the livers, which were then weighed to give the approximate wet weight. The lipid fraction was extracted from the ethanol and liver by maceration with light petroleum (b.p.40-60°C) in a Waring Blendor (Fisher *et al.*, 1952). After removal of the solvent on a steam bath under reduced pressure the extract was weighed to determine the total lipid.

The extract was analysed by the method of Fisher *et al.* (1952), involving the determination of total carotenoids by measurement of the absorption at 450 mμ in n–hexane, the chromatographic separation of vitamin A ester and alcohol, saponification of the two fractions, further chromatography to remove carotenoids, and finally estimation of vitamin A from the blue colour developed in the Carr-Price reaction and measured at 618 mμ. Values were calculated using the data for the Thompson direct-reading spectrophotometer recorded by Fisher *et al.* (1956). Although 618 mμ is the absorption maximum of the product of vitamin A_1 with antimony trichloride in chloroform, any vitamin A_2 present could have contributed to the total extinction measured at this wavelength. Since no measurements were made at 693 mμ, the absorption maximum for the product of vitamin A_2 and the reagent, it has not been possible to determine the extent to which vitamin A_2 interfered in the 618 mμ values. However, the indications are that only a small proportion of vitamin A_2 occurs in these livers; for example, Lambertsen & Braekkan (1956) found 9·5-12% vitamin A_2 in the liver vitamin A of *Squalus acanthias*, 9·5-10·5% in that of *Somniosus microcephalus* and 6% in that of *Raia oxyrhynchus*; also Pradhan & Magar (1956) found 4-8% vitamin A_2 in the vitamin A from livers of four species of shark from Indian waters.

RESULTS

The geometric mean concentrations and, in parentheses, the ranges of total lipids, vitamin A and carotenoids in all the livers analysed are given in Tables I and VII. Details of the results for each species are given in the following paragraphs in which the values for vitamin A are also compared with those of earlier workers.

Hexanchus griseus (Bonnaterre)—Six-gilled Shark

Livers from 11 fish were examined from 1954 to 1957. The fish were caught in February (2 ♀), July (1 ♂, 5 ♀), August (1 ♂, 1 ♀) and November (1 ♀), and ranged from 131 to 246 cm in overall length.

Of the females, 6 had livers with 50 μg vitamin A/g or less for fish of 163 to 234 cm, and 3 had livers with 95 to 137 μg/g for fish of 234 to 246 cm. Thus there is some accumulation of the vitamin during the life of the fish.

This species has a wide geographical distribution and its liver vitamin A content has been measured in other parts of the world, the following values being reported: 120-1470 μg/g liver and 300-2100 μg/g liver oil for the North Pacific (Swain, 1944), 42-190 μg/g liver and 72-1680 μg/g liver oil in South Africa (Molteno *et al.*, 1945), 995 μg/g liver and 1290 μg/g liver oil in the Philippines (Warfel & Clague, 1950), 637 μg/g liver oil in Italy (Monforte & Fenech, 1952), and 286 μg/g liver and 374 μg/g liver oil in Japan (Higashi *et al.*, 1953).

Carcharinus glaucus (L.)—Blue Shark

A female (229 cm) was taken in September 1958 and a male (138 cm) and a female (175 cm) in August 1954.

The vitamin A content (Table I) is of the same order as in fish from European waters (Demage & Mocoroa, 1946; Evers & Smith, 1933; Legendre & Lormand, 1941; Saviano, 1944-5), and New Zealand (Shorland, 1948, 1950) but lower than in those from South Africa (Molteno *et al.*, 1945), from California (Byers, 1940), from Oregon (Sinnhuber & Law, 1947), from Peru (Negrete, 1954) and from Japan (Higashi *et al.*, 1953; Ono *et al.*, 1952-3; Yamamura, 1956).

Cetorhinus maximus (Gunner)—Basking Shark

The livers of two immature male fish were analysed, one, 350 cm long, caught in November 1956, and the other, 427 cm long, in July 1959.

The vitamin A content of basking shark livers has usually been considered low. Bills *et al.* (1937) and Morgan *et al.* (1939) recorded the vitamin as absent from the livers of Pacific fish, although the latter workers also found 20 μg/g lipid by biological assay; Swain (1944) obtained values in the range 0-192 μg/g liver and 0-240 μg/g lipid and Sinnhuber & Law (1947) reported 56 μg/g liver and 65 μg/g lipid. Molteno *et al.* (1945) found no more than traces of vitamin A in livers of basking sharks from South African waters. Concentrations in livers of fish taken in European waters were a little higher than those in Table I (Davies & Worden, 1953-4; Demage & Mocoroa, 1946), but none of the values reported above would distinguish the liver of the basking shark as a rich source of vitamin A. On the other hand, Schmidt-Nielsen & Schmidt-Nielsen (1927) using a biological assay with rats obtained a value of 3000 μg/g liver oil, although in further experiments they failed to detect such high concentrations.

Eugaleus galeus (L.)—Tope

Livers were collected from twelve fish caught from 1954 to 1959, in January (3 ♂), February (1 ♂), May (1 ♀), June (1 ♂), October (3 ♂, 1 ♀) and December (1 ♂, 1 ♀). The fish, of which ten were adult and two approaching maturity, ranged from 124 to 160 cm in length. No correlation was detected between the concentrations of liver vitamin A, lipid or carotenoids and the size of fish, sex, or time of year.

TABLE II

DISTRIBUTION OF LIPID, VITAMIN A AND CAROTENOIDS IN LIVERS OF *EUGALEUS GALEUS* AND *LAMNA CORNUBICA*

Eugaleus galeus: Liver of adult female, 135 cm long; total weight of liver 472 g.

Part of liver	Weight (g)	Lipid (%)	Vitamin A μg/g liver	Vitamin A μg/g lipid	Carotenoids μg/g liver	Carotenoids μg/g lipid
Base, at junction of lobes	80	19	352	1880	0·7	3·7
Left lobe, middle cut	47	29	372	1271	1·7	5·9
Tip of left lobe	26	22	339	1506	3·2	14
Right lobe, middle cut	58	15	214	1410	0·8	5·5
Tip of right lobe	36	38	774	2050	2·1	5·6
Total	247	23	382	1655	1·4	6·0

Lamna cornubica: Liver of adult female, 213 cm long; total weight of liver not known.

Part of lobes	190	38	25	67	4·5	12
Extreme tips of lobes	45	24	68	284	9·5	40
Total	235	35	33	95	5·4	16

L. cornubica: Liver of adult female, 249 cm long; total weight of liver not known.

Junction of lobes	106	59	5·4	9·2	0	0
Middle of left lobe	57	58	3·4	5·9	1·6	2·8
Tip of left lobe	42	19	5·0	26	0·9	4·8
Middle of right lobe	65	49	13	26	5·1	10
Tip of right lobe	54	19	7·9	42	2·1	11
Total	324	45	6·9	15	1·8	4·0

The liver of the female tope caught in May 1956 was divided into several parts for separate analysis (Table II). Whereas the tip of the right lobe was richest in lipid and vitamin A, that of the left lobe had the highest concentration of carotenoids. Both vitamin A and lipid appeared to be more uniformly distributed in the left than in the right lobe.

Values for vitamin A in tope livers from Norwegian waters (Schmidt-Nielsen *et al.*, 1934*a*) and from the Bay of Biscay (Demage & Mocoroa, 1946) were of the same order as those now reported.

Lamna cornubica (Gmelin)—Porbeagle

Livers of 29 porbeagles were analysed from 1954 to 1959—in February (1 ♀), March (1 ♀), June (1 ♀), July (1 ♂, 4 ♀), August (3 ♂, 2 ♀), September (3 ♂), October (2 ♂, 1 ♀, 1 sex not recorded), November (5 ♂), and December (3 ♂, 1 ♀). The lengths of the fish, which included 24 adult or near adult and 5 immature fish, ranged from 94 to 262 cm. There was no apparent relationship between the size or sex of the fish or the time of the year and the liver reserves of vitamin A, lipid or carotenoids. The richest liver, containing 568 μg vitamin A/g, was obtained in October from a male fish of 211 cm, and the poorest, containing 6·5 μg/g, was taken in July from a female of 238 cm.

The livers of two fish were analysed in two or more parts (Table II). The tips were poorer in lipid than the main parts of the lobes in both livers. In the second liver the right lobe was richer in both vitamin A and carotenoids than the left.

Norwegian and Japanese workers have previously determined the vitamin A concentrations in porbeagle livers and all the ranges of values given, although overlapping to a considerable extent those in Table I, had higher minima and maxima; for example, 520-810 μg/g lipid (Schmidt-Nielsen & Schmidt-Nielsen, 1931), 782-1150 μg/g lipid (Schmidt-Nielsen *et al.*, 1934*a*), 2080 μg/g lipid (Higashi, 1941), and 120-15000 μg/g lipid (Yamamura, 1956).

Mustelus mustelus (L.)—Smooth Hound

Of three fish taken in January, May and December, 1955, the first was immature and 57 cm long and the others were adult, 83 and 91 cm long. The liver of the fish caught in May contained 80% lipid whereas those of the fish caught in winter had only 32 and 35%. On the other hand, these two fish had higher concentrations of carotenoids in their livers than the first. Liver vitamin A varied widely; the immature fish had the lowest concentration and the larger adult the highest. In fish caught in the Bay of Naples Saviano (1944-5) obtained values (66-69 μg/g) within the range now recorded.

Pristiurus melanostomus (Rafinesque)—Black-mouthed Dogfish

Fourteen fish of this species were collected from 1954 to 1959—in March (1 ♀), May (1 ♂), June (5 ♂, 1 ♀), July (2 ♂, 3 ♀), and December (1 ♀). Except for an immature male of 35 cm and a juvenile fish of 18 cm (caught in Loch Fyne in February 1962) all the fish, ranging from 51 to 77 cm, were adult or approaching their first maturity. The lowest concentrations of lipid and vitamin A occurred in the liver of the immature male taken in June 1959. The juvenile specimen was dissected into liver, alimentary canal and the rest of the fish and analysed as shown in Table III.

TABLE III

DISTRIBUTION OF LIPID, VITAMIN A AND CAROTENOIDS IN A JUVENILE *PRISTIURUS MELANOSTOMUS*

Organ	Lipid (%)	Vitamin A			Carotenoids		
		μg/g	μg/g lipid	% of total	μg/g	μg/g lipid	% of total
Liver	51	6·4	13	43	1·2	2·3	40
Alimentary canal	5·7	4·4	77	28	0	0	0
Rest of fish	0·76	0·41	54	29	0·17	22	60
Total	5·5	1·3	23	100	0·25	4·5	100

The recorded values for *P. melanostomus*, ranging from 4·1 to 16 μg vitamin A/g liver (Schmidt-Nielsen *et al.*, 1934*a*), are similar to those now reported.

Scyliorhinus caniculus (L.)—Lesser-spotted Dogfish

The 34 fish from which livers were analysed were caught from 1954 to 1959 during March (5 ♂, 7 ♀), June (4 ♂), August (1 ♀), September (2 ♂, 1 ♀), October (1 ♂, 8 ♀), and November (5 ♀). The fish, which ranged from 43 to 80 cm, included 27 adults and 7 immatures. Whereas the majority had vitamin A concentrations of 32 μg/g liver or less, those with higher concentrations were all fish of 64 cm or more in length. There appeared to be no relationship between vitamin A concentration and sex or season.

Three fish with carotenoid concentrations higher than 14 μg/g liver (two males with 44 and 95 μg/g and a female with 26 μg/g) were all large fish of 72 to 75 cm, thus indicating an accumulation of carotenoids with age. There was no apparent relationship between lipid concentration and size of fish or season.

The value of 900 μg vitamin A/g in the liver of *S. caniculus* from the Bay of Biscay, recorded by Demage & Mocoroa (1946), was well above the range reported here.

Centrophorus squamosus (Gmelin)—no common name

A spent female (125 cm) was caught in July 1956. Possibly because of the condition of the fish, the liver was relatively poor in both lipid and vitamin A compared with other selachians. Demage & Mocoroa (1946) reported somewhat higher concentrations of 32 μg vitamin A/g liver and 63 μg/g liver oil for this species from the Bay of Biscay.

Centroscyllium fabricii (Reinhardt)—Black Dogfish

An adult female (74 cm) was caught in May 1955. So far as is known the values for vitamin A, lipid and carotenoids in the liver are the first to be recorded.

Centroscymnus coelolepis Bocage & Capello—Portuguese Shark

One male (87 cm) was taken in May 1955 and another (96 cm) and a female (107 cm) in July 1956. No liver analyses appear previously to have been reported for this species.

Etmopterus spinax (L.)—no common name

Two fish (1 ♂, 1 ♀) were caught in May 1955, a female in August 1956, and the remainder (3 ♂, 6 ♀) in June 1959.

Vitamin A concentrations were considerably higher in the livers of the males than of the females and tended to increase with length and with maturity in both sexes. Carotenoid concentrations decreased with size and with maturity in both males and females. Schmidt-Nielsen *et al.* (1934*a*) gave values equivalent to 10-18 μg vitamin A/g liver and 15-20 μg/g liver oil for female fish analysed in Norway.

Scymnodon jonsonii (Jensen)—no common name

The values for the liver of an adult female (69 cm) caught in May 1955 appear to be the first recorded for this species.

Scymnorhinus licha (Bonnaterre)—"Darkie Charlie"

A mature female (141 cm) with large ova was taken in February 1956. The concentrations of lipid, vitamin A and carotenoids shown in Table I were derived from the combined analyses of the extreme tip of one lobe of the liver, weighing 38 g, and of the main part of the liver, weighing 228 g, the details of which are given below.

	Lipid (%)	Vitamin A		Carotenoids	
		μg/g	μg/g lipid	μg/g	μg/g lipid
Tip of lobe	84	67	80	1·6	1·9
Main lobe	64	39	61	0·51	0·79

They show that, in every respect, the tip was richer than the main lobe. Demage & Mocoroa (1946) recorded a value of 45 μg/g for vitamin A in the liver of this species from the Bay of Biscay.

Somniosus microcephalus (Schneider)—Greenland Shark

The smallest of the three fish was taken off East Greenland in July 1954, the largest (518 cm) in the same area in May 1955 and the third a female of 391 cm in the North Sea in April 1958. The largest fish had the highest concentrations of lipid and carotenoids and the lowest concentration of vitamin A in its liver. The complete liver of this specimen weighed approximately 400 lb (180 kg) and yielded 35 gallons (160 litres) of oil.

The values of liver vitamin A in *S. microcephalus* are similar to those already recorded for this species in the North Pacific—261 μg/g liver and 460 μg/g liver oil (Morton, 1944; Swain, 1944); in Ungava Bay, North-east Canada, 542 μg/g liver (Dunbar & Hildebrand, 1952); in Norway, 900-1200 μg/g liver oil (Lambertsen & Braekkan, 1956), and 228 μg/g liver and 632 μg/g liver oil (Schmidt-Nielsen *et al.*, 1934*a*); and variously in Arctic seas from East Greenland to the Barents Sea and Spitzbergen, 300-2700 μg/g liver oil (Aure & Kløkstad, 1951; Carlson, 1958).

Squalus acanthias L.—Piked Dogfish or Spur Dog

Specimens were collected from August 1954 to June 1959, in February (1 ♀), March (11 ♂, 11♀ all immature fish), June (5 ♂, 5 ♀), August (10 ♀, 5 ♂ foetuses, 1 ♀ foetus), September (5 ♂, 4 ♀), October 4 ♂, 4 ♀), November (14 ♂, 9 ♀).

Values up to 93 μg/g were recorded in fish of both sexes, ranging in length from 20 cm to 108 cm; nevertheless higher concentrations, from 145 to 1347 μg/g, were obtained in fish of 60 cm or over, thus indicating a possible relationship between size and liver vitamin A reserves. The highest concentrations of vitamin A occurred in the livers from June to October, but this might be associated with the fact that the fish examined at this time of the year, apart from the foetuses, were generally larger than those sampled in February, March and, to some extent, November. Vitamin A concentrations in the livers of the foetuses were low, but of the same order as in those of many maturing and mature fish. Mean values for vitamin A (μg/g) and carotenoids in the different maturity groups were determined as in Table IV.

TABLE IV

COMPARISON OF VITAMIN A AND CAROTENOID CONCENTRATIONS AT DIFFERENT STAGES OF MATURITY IN *SQUALUS ACANTHIAS*

	Sex	Foetus	Immature	Maturing	Adult
Vitamin A					
mean values	♂	5·4	22·4	35·0	162·4
μg/g liver	♀	2·1	18·8	33·7	98·3
Carotenoids					
mean values	♂	0·0	2·4	2·8	4·2
μg/g liver	♀	2·7	3·8	3·0	3·7

It would appear from these figures that vitamin A concentration increases with maturity in both males and females. Carotenoid concentration also increases with maturity in the males but in the females the concentration would seem to reach a steady level at an early stage.

Lipid concentrations did not appear to be related to size or season.

The detailed distribution of vitamin A, lipid and carotenoids was determined in the liver of one specimen, a female from which some of the foetuses mentioned above had been removed (Table V).

TABLE V

DISTRIBUTION OF LIPID, VITAMIN A AND CAROTENOIDS IN A LIVER OF *SQUALUS ACANTHIAS*

Liver of an adult ♀ fish, 80-90 cm long. Whole liver analysed in portions

			Vitamin A		Carotenoids	
Part of liver	Weight (g)	Lipid (%)	μg/g liver	μg/g lipid	μg/g liver	μg/g lipid
Proximal half of right lobe	43	26	1539	6010	6·7	26
Distal half of right lobe	51·5	9·9	1225	12370	3·6	37
Total for right lobe	94·5	17	1366	8020	5·0	30
Proximal half of left lobe	42·5	44	46	106	6·4	15
Distal half of left lobe	42	30	2626	8760	6·0	20
Total for left lobe	84·5	37	1316	3568	6·2	17
Total for whole liver	179	26	1347	5100	5·6	21

Lipid concentrations in the right lobe were lower than in the left and considerable differences in vitamin A concentration occurred within the lobes, especially in the left. However, the mean concentrations in each lobe were closely similar.

It is not surprising in view of its wide distribution that so common a species has attracted more attention from earlier workers than other fish dealt with in this paper. Table VI summarises the results of other workers and those now reported.

TABLE VI

COMPARISON OF VALUES REPORTED FOR VITAMIN A IN THE LIVER OF *SQUALUS ACANTHIAS*

	Vitamin A		
Locality	μg/g liver	μg/g lipid	References
British waters	—	188-647	Evers & Smith, 1933
Norway	55-332	112-832	Schmidt-Nielsen *et al.*, 1934*a*
,,	—	450	Lunde, 1938-9
,,	—	180	Lambertsen & Braekkan, 1956
Newfoundland	—	264-1240	Templeman, 1944
Western North Atlantic	—	76-6300	Wood & Johnston, 1944
New England coast	—	690	Holmes *et al.*, 1941
Azov—Black Sea basin	42-378	—	Dragunov & Kasinova, 1949, 1951; Perepletshik, 1951
Black Sea	75-3288	—	Vinogradova, 1953, 1957
Far Eastern waters, U.S.S.R.	9-2820	45-5850	Kizevetter & Lagovskaya, 1951
Scottish waters	1·3-1347	4·7-7460	This paper

Squatina squatina (L.)—Angel Fish

Liver samples were analysed from ten specimens (69-135 cm) from 1954 to 1962—in January (1 ♀), February (2 ♀), April (2 ♀), May (3 ♀), September (1, sex not recorded) and October (1 ♂). The range of vitamin A concentrations in immature and maturing fish was 7·2-57 μg/g liver and in adult fish 42-87 μg/g. No regularity was apparent in the lipid and carotenoid concentrations. Other values for vitamin A in this species are 81 μg/g liver and 201 μg/g liver oil for fish from the Bay of Biscay (Demage & Mocoroa, 1946).

TABLE VII

LIPID, VITAMIN A AND CAROTENOIDS IN THE LIVERS OF SKATES AND RAYS AND OF *CHIMAERA MONSTROSA*

Species	Sex	No. of livers analysed	Liver lipid (%)	Vitamin A		Carotenoids	
				μg/g liver	μg/g lipid	μg/g liver	μg/g lipid
Myliobatis aquila	♀	2	25 (19-34)	4·6 (1·4-15)	23 (7·8-43)	2·5 (2·3-2·8)	11 (8·5-13)
Raia batis	♂	19	27 (8·4-88)	21 (1·1-619)	73 (7·1-2930)	5·6 (1·2-14)	21 (4·0-87)
	♀	24	29 (5·8-89)	15 (0·5-195)	57 (2·8-1020)	7·9 (2·2-21)	28 (4·6-113)
Raia brachyura	♂	8	28 (23-36)	17 (4·1-53)	62 (14-171)	3·8 (0-8·0)	12 (0-28)
	♀	4	34 (23-53)	14 (3·5-49)	41 (12-216)	1·8 (0-3·1)	3·8 (0-10)
Raia circularis	♂	1	80	38	48	11	14
	♀	4	34 (20-54)	32 (9·2-134)	92 (17-406)	2·5 (1·1-6·1)	7·3 (2·9-19)
Raia clavata	♂	13	36 (22-67)	41 (3·0-282)	113 (8·7-1292)	9·6 (5·5-18)	26 (9·9-77)
	♀	10	33 (18-44)	40 (9·5-171)	124 (28-491)	8·3 (4·8-12)	26 (12-51)
Raia fullonica	♂	4	47 (37-71)	18 (3·4-70)	38 (9·0-151)	5·2 (1·5-35)	11 (3·3-94)
	♀	8	57 (33-80)	18 (8·6-34)	32 (16-100)	2·2 (0·9-5·2)	3·9 (1·5-11)
Raia lintea	♂	2	41 (26-65)	102 (72-144)	248 (111-553)	1·4 (1·2-1·6)	3·4 (2·5-4·5)
	♀	2	44 (35-56)	33 (27-40)	74 (48-115)	0·8 (0·8-0·9)	1·9 (1·4-2·6)
	not known	2	31 (22-43)	115 (64-208)	378 (148-966)	1·2 (0·8-1·7)	3·7 (1·7-8·1)
Raia montagui	♂	9	29 (12-52)	36 (1·0-194)	127 (1·9-1675)	6·0 (0-10)	16 (0-52)
	♀	5	22 (6·3-47)	7·1 (1·0-72)	33 (12-153)	7·3 (3·5-22)	33 (9·4-102)
Raia naevus	♂	20	28 (1·0-84)	27 (2·1-504)	97 (16-1645)	7·4 (1·9-25)	26 (3·8-1000)
	♀	11	36 (8·3-73)	21 (1·4-269)	59 (4·8-620)	8·9 (0-24)	17 (0-56)
Raia oxyrhynchus	♂	2	66 (65-68)	33 (18-62)	50 (26-96)	2·2 (1·3-3·6)	3·3 (2·0-5·3)
	♀	2	42 (39-46)	22 (13-38)	52 (33-88)	1·5 (1·0-2·2)	3·5 (2·5-4·8)
Raia radiata	♂	13	14 (2·1-85)	11 (1·1-152)	69 (1·9-7210)	9·5 (4·7-36)	47 (6·1-1520)
	♀	15	18 (5·4-64)	21 (4·4-513)	113 (12-2460)	8·0 (2·7-29)	44 (5·1-418)
Torpedo nobiliana	♂	1	53	28	52	1·2	2·3
	♀	8	57 (46-65)	23 (8·3-48)	39 (14-81)	2·9 (1·1-8·2)	5·0 (1·9-14)
Trygon pastinaca	♀	5	25 (8·9-70)	11 (2·0-84)	42 (12-134)	13 (7·5-22)	54 (32-124)
Chimaera monstrosa	♂	2	31 (21-46)	7·5 (5·9-9·5)	24 (13-46)	8·4 (8·3-8·4)	27 (18-40)
	♀	3	42 (31-61)	4·1 (1·0-14)	11 (2·6-47)	7·1 (4·1-13)	17 (10-43)

Myliobatis aquila (L.)—Eagle Ray

Livers were analysed from two specimens caught in December 1957 and November 1958; these fish were 57 and 52 cm respectively measured across the disc. The concentrations of vitamin A (Table VII) were lower than for other skates and rays and the earlier values, 56-851 μg/g liver oil, for this species in Argentine waters (Castellanos, 1939).

Raia batis L.—Blue Skate

More livers of *R. batis* were analysed than of any other species of *Raia*. The fish, measuring across the disc from 15 to 165 cm, were collected from August 1954 to July 1959—in January (5 ♂, 5 ♀), March (2 ♀), May (1 ♂), June (3 ♂, 4 ♀), July (1 ♂, 1 ♀), August (3 ♂, 1 ♀), September (2 ♂, 5 ♀), October (4 ♂, 5 ♀) and November (1 ♀).

The concentrations of vitamin A in the liver covered a wider range in the larger fish than in the smaller specimens, and the largest of them all, a male of 165 cm across the disc, taken in August, gave 619 μg vitamin A/g liver, over three times the next highest value. The values in fish of both sexes caught in January were strikingly low, 14 μg vitamin A/g liver or less, except in one male (82 cm breadth) which gave 112 μg/g. These fish were taken in different parts of the North Sea in January 1955 and, with the exception of the male just mentioned, ranged from 20 to 62 cm across the disc; with two exceptions they were immature.

Although no relationship between sex or season and liver lipid concentration was apparent, a tendency for lipid reserves to increase with size and therefore with age was observed in this species. Carotenoid concentrations did not appear to be related to sex, size or season. As Table VIII shows, both lipid and vitamin A concentration increased with advancing maturity. On the other hand carotenoid concentrations decreased.

TABLE VIII

COMPARISON OF LIPID, VITAMIN A AND CAROTENOID CONCENTRATIONS AT DIFFERENT STAGES OF MATURITY IN *RAIA BATIS*

	Sex	Immature	Maturing	Adult
Lipid				
mean value g/100g	♂	20·8	34·2	40·4
	♀	20·3	30·1	44·1
Vitamin A				
mean value μg/g	♂	5·3	33·4	56·8
	♀	10·3	14·4	33·3
Carotenoids				
mean value μg/g	♂	8·4	7·9	3·5
	♀	10·3	8·3	5·6

The liver lobes of 3 fish caught in October 1956 were analysed separately and Table IX shows the marked differences in the lipid concentrations between the right and left lobes and the less marked variations in the vitamin A concentration. Carotenoid concentrations did not exhibit these variations between lobes to the same degree.

TABLE IX

DISTRIBUTION OF LIPID, VITAMIN A AND CAROTENOIDS IN LIVERS OF *RAIA BATIS* AND *R. FULLONICA*

All 4 fish caught east of Sydero, Faroe Islands, 25th October, 1956

			Vitamin A		Carotenoids	
Part of liver	Weight (g)	Lipid (%)	μg/g liver	μg/g lipid	μg/g liver	μg/g lipid
(a) *Raia batis*. Liver of a maturing ♂ fish, 74 cm in breadth.						
Right lobe	167	35	57	163	9·6	28
Left lobe	161	76	83	109	6·9	9·0
Whole liver	328	55	70	127	8·2	15
(b) *Raia batis*. Liver of a maturing ♂ fish, 78 cm in breadth.						
Right lobe	152	31	33	106	6·4	21
Left lobe	171	3·0	7·4	251	5·3	178
Whole liver	323	19	19	120	5·8	36
(c) *Raia batis*. Liver of a maturing ♀ fish, 79 cm in breadth.						
Right lobe	230	58	41	71	8·3	14
Left lobe	232	7·8	29	366	9·8	125
Whole liver	462	33	35	106	9·1	28
d) *Raia fullonica*. Liver of a maturing ♀ fish, 70 cm in breadth.						
Right lobe	87	20	16	80	2·3	12
Left lobe	62	51	60	118	5·1	10
Whole liver	149	33	34	100	3·5	11

Vitamin A concentrations previously recorded by Evers & Smith (1933), 25-695 μg/g oil, and by Lovern *et al.* (1939), 70 μg/g liver, in *R. batis* from British waters, and by Schmidt-Nielsen *et al.* (1934*a*), 55-338 μg/g liver and 258-735 μg/g liver oil, from the Norwegian coast, lie within the range of the concentrations derived from the present analyses.

Raia brachyura Lafont—Blonde Ray

Five fish (3 ♂, 2 ♀) were taken in March 1956, one (♀) in April 1956, one (♀) in July 1956 and five (all ♂) in June 1959. These fish, measuring 28 to 74 cm across the disc, were immature with the exception of one adult female of 74 cm. The largest male had the highest concentrations of vitamin A and carotenoids but otherwise no relationship was evident between concentrations of these substances or lipid and sex, size or season. No previous study of these substances in *R. brachyura* appears to have been made.

Raia circularis Couch—Sandy Ray

Adult female fish measuring 55 to 73 cm across the disc were taken in August 1954 (1), in March 1956 (1) and in July 1956 (2); a single adult male (57 cm) was caught in July 1956. Lipid, vitamin A and carotenoid analyses were too few for any tendencies to be observed. No previous studies on this species have been traced.

Raia clavata L.—Thornback Ray

Twenty-three specimens measuring from 29 to 73 cm across the disc were caught from 1954 to 1959—in January (1 ♂), February (1 ♂), June (8 ♂, 4 ♀), July (1 ♀), August (3 ♀), September (1 ♂, 1 ♀) and October (2 ♂, 1 ♀).

As in some of the previous species the range of liver vitamin A concentrations tended to be greater in the larger fish, but no comparable trend was observed for lipid or carotenoids. As the material was predominantly summer-caught no seasonal trend was detectable.

Earlier research on vitamin A in *R. clavata* has related to fish from British waters (Lovern *et al.*, 1933), from South Africa (Molteno, 1938), and from the Azov and Black Seas (Dragunov & Kasinova, 1949, 1951; Kuznetsova, 1953; Perepletshik, 1951; Petrov, 1948, and Vinogradova, 1951, 1953, 1957). The results of these workers lie within the ranges of the present work given in Table VII.

Raia fullonica L.—Shagreen Ray

Livers were analysed from 12 fish collected in June (6 ♀), July (2 ♂), August (1 ♂), October (1 ♀) and November (1 ♂, 1 ♀) between 1954 and 1959. Disc measurements ranged from 39 to 70 cm and with the exception of one adult male all the fish were immature or maturing.

In general, lipid concentrations in the livers were higher in the female fish than in the males, and did not appear to be related to size or season. Vitamin A concentrations in the livers were more variable in the males than in the females, but no trends were detected relating the results to size or season. One male fish with only 3·4 μg vitamin A/g liver had a carotenoid concentration of 35 μg/g liver, which was considerably higher than in the others of either sex. In one liver of which the lobes were analysed separately, the left lobe was richer in lipid, vitamin A and carotenoids than the right (Table IX). The values obtained for vitamin A in the livers of *R. fullonica* in Norway by Schmidt-Nielsen *et al.* (1934*a*) were 11-178 μg/g liver and 31-495 μg/g liver oil.

Raia lintea Fries—no common name

Five of these fish were caught in September 1954 and one in May 1955. Breadth ranged from 57 to 76 cm.

There was some indication that the livers of the males were richer in vitamin A and carotenoids but judgment must be reserved on evidence from such small numbers. No similar work has hitherto been reported for *R. lintea*.

Raia montagui Fowler—Spotted Ray

Fourteen fish were collected during three cruises, four (♂) in March 1956, one (♂) in July 1956, and nine (4 ♂ and 5♀) in June 1959. Apart from a very young specimen 8 cm in breadth, with the yolk-sac still attached, the males ranged in breadth from 23 to 58 cm and the females from 17 to 47 cm.

With few exceptions the males had higher concentrations of vitamin A in their livers than the females and the highest concentrations were found in the largest fish of both sexes.

The juvenile male had a vitamin A concentration of 21 μg/g liver, but no measurable carotenoids. Lipid and carotenoid concentrations in the other livers appeared to be unrelated to size, sex or season. Edisbury *et al.* (1938) reported 7·0μg vitamin A/g liver for this species, referred to in their paper as *Raia maculata*.

Raia naevus Müller & Henle—Cuckoo Ray

Livers were analysed from 31 fish, measuring from 9 to 39 cm across the disc, and collected from 1954 to 1959—in January (3 ♂, 2♀), March (5 ♂, 2 ♀), June (4 ♂), July (1 ♀), August (1 ♂), September (3 ♀), October (5 ♂, 2 ♀) and November (2 ♂, 1 ♀).

As in some of the species already described, the livers with the richest concentrations of vitamin A came from the larger fish. Most of the smaller fish were caught in January or March, but the occurrence of low concentrations of liver vitamin A in those months may be related to size rather than to any seasonal effect. Liver lipid concentrations also tended to increase with the size of the fish, but carotenoids usually occurred in lower concentrations in the larger fish.

Values previously reported for livers of *R. naevus* from the Bay of Biscay were 24-33 μg vitamin A/g liver and 96-105 μg/g liver oil (Demage & Mocoroa, 1946).

Raia oxyrhynchus L.—Long-nosed Skate

Two female fish, breadth 93 and 127 cm, were taken in June 1955 and in July 1956, and two males, 84 and 85 cm, in August 1954 and July 1955, respectively. Vitamin A concentrations of 32-96 μg/g liver and 59-258 μg/g liver oil (Schmidt-Nielsen *et al.*, 1934*a*) and of 45 μg/g liver oil (Lambertsen & Braekkan, 1956) have been reported for *R. oxyrhynchus* in Norway, and higher values of 205-241 μg/g at Naples by Saviano (1944-5).

Raia radiata Donovan—Starry Ray

Twenty-eight specimens, measuring 12·5 to 35 cm in breadth were caught from 1954 to 1958—in January (2 ♂, 3 ♀), February (2 ♂, 1 ♀), March (3 ♂, 5 ♀), July (1 ♀), August (2 ♂, 1 ♀), September (1 ♂) and October (3 ♂, 4 ♀).

The range of vitamin A concentration in the livers of the larger fish was greater, with a very high value of 513 μg/g, for the largest female. Liver vitamin A reserves were apparently unrelated to sex. Liver lipid concentrations also showed a bigger range of values for the larger fish. Carotenoid concentrations did not appear to be related to sex or to size.

Schmidt-Nielsen *et al.* (1934*a*) recorded vitamin A concentrations of 11-233 μg/g liver and 54-457 μg/g liver oil in male fish in Norway.

Torpedo nobiliana Bonaparte—Electric Ray

Liver samples were collected from nine fish caught from 1954 to 1959. These fish ranged in length from 66 to 99 cm, and were taken in February (1 ♀), April (2 ♀), June (1 ♀), September (1 ♂, 2 ♀), and December (2 ♀). No previous analyses have been reported on this species.

Trygon pastinaca (L.)—Sting Ray

Five females, measuring in breadth from 25 to 52 cm, were taken in January and November 1955, in August and November 1956, and in February 1960.

The highest concentrations of vitamin A and lipid occurred in the liver of the largest fish; carotenoid concentration also increased with the size of the fish. Livers of *T. pastinaca* had previously been analysed by a number of workers in other countries; for fish from the Azov and Black Seas values of 18-24 μg vitamin A/g liver and 60-225 μg/g liver oil (Dragunov & Kasinova, 1949, 1951; Perepletshik, 1951; Kuznetsova, 1953) and 31-1087 μg/g liver (Vinogradova, 1953, 1957) have been reported. Petrov (1948) found concentrations of 150-313 μg/g liver oil in this species also in the U.S.S.R. In fish from the Bay of Biscay, Demage & Mocoroa (1946) reported concentrations of 19 μg vitamin A/g liver and 90 μg/g liver oil, whereas Espil & Fleury (1945) had obtained higher values of 330-584 μg/g liver oil. For *Trygon violacea*, presumed to be synonymous with *T. pastinaca*, from Naples, Saviano (1944-5) reported vitamin A concentrations of 89-272 μg/g liver.

Chimaera monstrosa L.—Rabbit Fish

Five livers were analysed (Table VII) from fish caught in July 1956. The females of 47, 81 and 92 cm length were immature, maturing and adult respectively; the males of 54 and 70 cm were immature and maturing. Vitamin A and carotenoid concentrations increased with the size of the fish, except in the adult which had values lower than in either of the maturing fish.

Previous analyses gave 45-90 μg vitamin A/g liver oil in Norway (Schmidt-Nielsen & Schmidt-Nielsen, 1930*b*), but only a trace was found for the same species in South Africa (Molteno *et al.*, 1945).

DISCUSSION

It is obvious from the foregoing results that in most species the spread of values of lipid, vitamin A and carotenoid concentrations increases with the number of livers analysed. In general, the livers of sharks and dogfishes are richer in lipid and vitamin A and poorer in carotenoids than those of skates and rays, these differences probably being related to the kind of food eaten. With the exception of the basking

shark, the larger sharks are richest in the vitamin, which they probably derive from their food which consists predominantly of teleost fishes and to a less extent cephalopods (Day, 1880-84; Hardy, 1959; B. B. Rae—personal communication). One species of dogfish which preys on a wider range of food types is the lesser-spotted dogfish *Scyliorhinus caniculus*. The diet of this fish includes appreciable quantities of fish, molluscs and decapod crustaceans (Rae—personal communication). This may possibly account for the somewhat higher concentration of carotenoids found in their livers.

The basking shark feeds on plankton including larval and post-larval fishes and crustaceans such as copepods and euphausiids. Matthews & Parker (1950) refer to the basking shark as "clearly an indiscriminate plankton feeder, and the principal constituent of the food will be the dominant constituent of the plankton at any particular time and place". These workers do not mention any planktonic animal larger than *Calanus*, but it is possible that euphausiids are eaten when they occur in the plankton. Nevertheless, basking sharks do not appear to eat enough of this type of food to enable them to accumulate the rich vitamin A reserves of these crustaceans in their livers.

The medium-sized and larger skates are mainly fish-eaters, whereas the young forms of all skates and the adults of the smaller species such as *Raia radiata* feed mainly on Crustacea such as crabs and shrimps (Rae—personal communication). Molluscs, polychaetes and brittle-stars have also been found in the stomachs of some skates and of the rabbit-fish. These invertebrates contain a greater variety and concentration of carotenoid pigments than is found in free-swimming crustaceans such as euphausiids which are eaten by pelagic fish, and this would seem to account for the richer reserves of carotenoids in the livers of skates, rays and *Chimaera* than in those of sharks and dogfishes (Fisher *et al.*, 1952, 1955, 1956).

The distribution of vitamin A within the liver has been discussed by Higashi (1961), who mentions that some Japanese workers have found that dogfish liver is richer in vitamin A at the posterior end of the liver than at the anterior end and that the liver is also richer internally than externally. Whereas there are some examples of distal portions being richer than proximal ones in Tables II and V, other values in the same Tables show the reverse. Differences between right and left lobes are also inconsistent in Tables II, V and IX and do not appear to be related to asymmetry of the internal organs as suggested by Higashi (1961).

Although many of the livers examined were rich in oil, none of them is sufficiently rich in vitamin A to be comparable with some teleost fishes or with the soupfin shark *Galeorhinus zyopterus* on the Pacific coast of the United States and Canada (Byers, 1940; Ripley & Bolomey, 1946; Sinnhuber & Law, 1947; Swain, 1944) or with the black-finned shark *Carcharinus melanopterus* of the Indian Ocean and Philippine seas (Das *et al.*, 1949, 1950; Molteno *et al.*, 1945; Warfel & Clague, 1950).

SUMMARY

1. Lipid, vitamin A and carotenoid concentrations were measured in 230 livers from 17 species of sharks and dogfishes, in 194 livers from 13 species of skates and rays, and in 5 livers of the rabbit-fish.

2. Lipid and vitamin A concentrations tended to be higher and carotenoid concentrations lower in shark and dogfish livers than in those of skates and rays. All three substances exhibited wide ranges of concentration in the same species.

3. Tope livers were richer in vitamin A than those of any other species. Those of the blue shark and Greenland shark also had fairly high concentrations of the vitamin, but none is considered to be of outstanding commercial value.

4. There is evidence that in some species the richest concentrations of lipid and vitamin A occurred in the larger fish. No consistent evidence of differences associated with sex or season was observed in any species, but increased concentrations of vitamin A with increasing maturity were noted in both male and female *Squalus acanthias*. Similarly increases in the concentration of lipid and vitamin A were also noted to accompany advancing maturity in *Raia batis*, while at the same time a slight decline in the carotenoid concentration was observed in this fish.

5. The possible effect of the food organisms eaten by the different species on their reserves of lipid, vitamin A and carotenoids is briefly discussed.

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